# Initial response of Orthoptera to beaver (*Castor fiber*) reintroductions in post-arable enclosures

Tim Gardiner[1], Emily Crisp[1]

1 Fisheries, Biodiversity and Geomorphology, Environment Agency, Iceni House, Cobham Road, Ipswich, Suffolk, IP3 9JD, UK.

Corresponding author: Tim Gardiner (tim.gardiner@environment-agency.gov.uk)

Academic editor: Axel Hochkirch | Received 3 April 2025 | Accepted 28 May 2025 | Published 25 June 2025

https://zoobank.org/1E9F5658-393B-4FB3-B7C7-08F19EA26C6D

Citation: Gardiner T, Crisp E (2025) Initial response of Orthoptera to beaver (*Castor fiber*) reintroductions in post-arable enclosures. Journal of Orthoptera Research 34(2): 213–222. https://doi.org/10.3897/jor.34.154843

## Abstract

Rewilding aims to restore 'self-willed' ecosystems involving the creation of habitat subject to stochastic disturbance, connected by favorable corridors for dispersal of animals including insects. Herbivores such as the Eurasian beaver *Castor fiber* (Linnaeus, 1758) have been reintroduced in the UK to promote natural flood management as part of a rewilding strategy. At Spains Hall in Finchingfield (south-east England), beavers were released into two large enclosures (both c. 20 ha) in March 2023 which were concurrently reverting from arable farmland to riparian meadow. Monitoring of Orthoptera 15–18 months after release in June-September 2024 revealed statistical evidence that the abundance of the two localised groundhoppers, *Tetrix subulata* (Linnaeus, 1758) and *Tetrix undulata* (Sowerby, 1806), and the lesser marsh grasshopper *Chorthippus albomarginatus* (De Geer, 1773), was higher in the beaver enclosure meadows than in the control plots. The Essex Red Data List species, the common green grasshopper *Omocestus viridulus* (Linnaeus, 1758), was also recorded within the beaver meadows. The damming of the watercourse in one enclosure led to the creation of new off-line lotic channels and wet ground which were important for these species, particularly bare mud margins which were used by groundhoppers (Tetrigidae). There was also evidence that meadows on the east side of the river had a greater abundance of long-winged conehead *Conocephalus fuscus* (Fabricius, 1793) and *T. subulata* than the west, perhaps due to the sheltered microclimate and wetland features on this side of the channel, particularly in the beaver enclosures. We conclude that in enclosures on former arable farmland Orthoptera may respond to damming which quickly creates beaver meadows in flooded areas within the first two years of release. However, only one enclosure had dams in this study so the effects of beavers may be dependent on variables such as habitat quality and watercourse characteristics.

## Keywords

Acrididae, bush-cricket, grasshopper, groundhopper, natural flood management, Tetrigidae, Tettigoniidae, rewilding

## Introduction

To reverse the decline of insects such as grasshoppers and bush-crickets, rewilding of arable farmland may be highly beneficial (Tree 2017, van Klink and WallisDeVries 2018, Garrido et al. 2022). The ideal aim of rewilding is to restore natural processes, often involving the creation of large areas of habitat subject to stochastic disturbance connected by favorable corridors for species to disperse along (Carver and Convery 2021, Gordon et al. 2021a, b). Rewilding is well established at UK sites such as Knepp in West Sussex (Greenaway 2006, Wallace 2018, Dempsey 2021) and three sites in Suffolk – Arger Fen, Black Bourn Valley and the Somerleyton Estate (Gardiner and Casey 2022a, b, 2024). Research at Black Bourn Valley revealed that Orthoptera were in higher abundance and diversity in fields >8 years post-arable cropping cessation with riparian wet meadows being a key source of colonising insects (Broad 2023, Gardiner and Casey 2022a, b). Herbivores have a significant role in modifying vegetation structure and introducing habitat heterogeneity into former arable river valleys, especially lagomorphs (Gardiner and Casey 2022a, b). Herbivores such as the Eurasian beaver *Castor fiber* (Linnaeus, 1758) also have significant impacts on habitats and species in riparian landscapes (Wright et al. 2002, Campbell-Palmer et al. 2015, Campbell-Palmer et al. 2016). In Europe, beaver numbers declined to just 1200 individuals in the 20$^{th}$ century before recovering to over 1.2 million animals in 2020 due to the success of reintroduction programs (Wrobel 2020, Halley et al. 2021). Beavers have been reintroduced in the UK to promote natural flood management (NFM; Forbes et al. 2015).

Beavers became extirpated from the UK during the 16$^{th}$ century after the last known British record in 1526-7 (Raye 2015). Beavers are ecosystem engineers leading to significant modifications to river corridor structure, geomorphology, nutrient cycling and the storage of water on the floodplain (Rosell et al. 2005, Cunningham et al. 2007, Willby et al. 2018, Brazier et al. 2021, Larsen et al. 2021). Dam building and foraging on woody and herbaceous vegetation are the main beaver behaviours that influence river corridors and their biodiversity value (Law et al. 2014, Campbell-Palmer et al. 2015). Dam building leads to higher water levels and diversity of flow in river channels (Wright et al. 2002, Campbell-Palmer et al. 2016), while beaver lodges can also become biodiversity hotspots in this environment with a high degree of habitat heterogeneity (Wilson and Bremner 2025).

Geomorphological and hydrological reactions to beaver presence have been studied (Hering et al. 2001), as have the positive effects on amphibians (Romansic et al. 2020), bats (Hooker et al. 2024) and aquatic macro-invertebrates (Nummi 1989, Bush and Wissinger 2016). Less well known is the impact of beaver dam building and foraging on the abundance and diversity of terrestrial invertebrates in riparian habitats. The studies that exist have focused on increases in flying insects and moth diversity (Andersen et al. 2023), true bugs (Orazi et al. 2022) and saproxylic beetle assemblages associated with dead wood habitats established due to the felling activities and flooding associated with beavers (Zahner et al. 2006, Horak et al. 2010, Mourant et al. 2018). Away from wooded beaver habitats, a single study of Orthoptera in beaver clearings in Germany has been undertaken (Dalbeck 2011).

Dalbeck's study focused on the presence or absence of Orthoptera in open beaver clearings (several hectares in size), recording 14 species, but noting the absence of otherwise abundant species such as Roesel's bush-cricket *Roeseliana roeselii* (Hagenbach, 1822), possibly due to unsuitable, short vegetation structure. The relatively species-rich beaver clearings in the Eifel Mountains were populated by c. 18% of the native Orthoptera of Germany (Fartmann et al. 2024) including stenotopic insects such as large marsh grasshopper *Stenophyma grossum* (Linnaeus, 1758) which require differing environmental niches (Dalbeck 2011).

Given the propensity in the UK for insects such as slender groundhopper *Tetrix subulata* (Linnaeus, 1758) to benefit from wet bare ground on the edges of ponds on riparian rewilding sites developing on former arable fields (e.g. Black Bourn Valley, Gardiner and Casey 2022a, b), it is likely that these species may respond rapidly to early successional stages of wetland creation from the damming activities of beavers and any increase in habitat heterogeneity (e.g. formation of beaver meadows within first two years of beaver release). Dalbeck (2011) only recorded the presence or absence of Orthoptera and did not quantify the abundance or diversity of beaver clearings. The raising of water levels by impounded river water behind a dam, can lead to the formation of riparian beaver meadows where flooding occurs (Stringer and Gaywood 2016). In the first 1–2 years of beaver meadow development, wet grassland with puddles can form, with a mosaic of shallow mud shores on the marsh edge interspersed with taller vegetation (Andersen et al. 2024).

At Spains Hall in Finchingfield, south-east England, beavers were reintroduced to former arable land reverting naturally to open floodplain grassland and scrub mosaics. The two fenced enclosures were established in early 2023 and represented an excellent opportunity to monitor the early development of beaver meadows within their first two years in a different context to the forest clearings of Dalbeck (2011) in Germany. Orthoptera diversity is low in north Essex due to the prevalence of intensive arable farming (i.e. high inorganic fertiliser and pesticide usage) and improved grassland which supports 7–11 species compared to the extensive grazed marshland and flood embankments of the coast (13–18 species, Fargeaud and Gardiner 2018). Therefore, the Spains Hall beaver enclosures and their developing post-arable grasslands could enhance Orthoptera abundance and diversity in an otherwise inhospitable landscape for insects or their isolation in an arable landscape may render colonisation slow or non-existent for less mobile species.

The aim of this paper is to report a study on the orthopteran assemblages of riparian grassland in fenced beaver enclosures at Spains Hall, Finchingfield, in Essex, UK two summers after reintroduction. Results, specifically the abundance and diversity of Orthoptera, are discussed in relation to the damming activities of beavers in the two enclosures compared to adjacent control meadows.

## Materials and methods

*Study site.*—Spains Hall Estate in Finchingfield, south-east England (latitude/longitude 51°58'52.0356"N, 0°27'9.6516"E) is a mosaic of lowland woodland, open farmland, old grassland, orchard and river valley (c. 800 ha total area). In 2019, beavers (one adult male and one female) were introduced into a 4 ha woodland area (The Moors) as part of a NFM scheme to store water and reduce flooding to the village of Finchingfield. Damming by beavers in The Moors has led to the storage of c. 2.4 million litres of water on the floodplain (Brown 2022). This unprecedented project by the Spains Hall Estate is jointly supported by a public and private partnership which includes Anglian Water, Environment Agency, Anglian Eastern Regional Flood and Coastal Committee (RFCC), Essex County Council and Essex and Suffolk Water.

The beaver reintroduction scheme was expanded in 2023 with the release of a pair of beavers (one adult male and female) into two large fenced enclosures (both c. 20 ha, Table 1) along the tree-lined river, Finchingfield Brook (river channel width bank top to bank top c. 2–4 m, water depth <1 m), which were formerly arable farmland (cropping ceased after 2018; Brown 2022) and are in the process of natural reversion to grassland floodplain meadows. The fields in the enclosures were previously cropped for agriculture with nitrogen (N) fertiliser applied to a range of crops including spring barley, winter beans and winter wheat. Soil types vary from clay loams with impeded drainage and freely drained sands/gravels. The intention of reverting the arable fields in the enclosures was to create natural wetland habitats alongside the river through the damming behaviour of beavers, storing water on the floodplain. Grazing ungulates (deer) were removed from the enclosures before the release of beavers to ensure no overgrazing of enclosure habitats.

Narrow strips of grassland were present along Finchingfield Brook during the time of arable cropping, allowing some Orthoptera habitat to remain within the intensive arable cropping regime which would otherwise be highly unfavorable for insects (Gardiner et al. 2002). It is likely that after arable cropping ceased that Orthoptera colonised any reestablishing grassland before the enclosures were created. Therefore, this study measures the alteration of the reestablishing grassland by beaver activities and its effects on Orthoptera compared to control grasslands outside of the enclosures.

To contrast with the two fenced beaver enclosures, two unfenced open meadow control sites were selected for this study without beavers, Control A adjacent to the south of Enclosure A and Control B, immediately to the north of Enclosure B (Table 1, Figs 1, 2). The enclosure fences may influence the behaviour of grazing ungulates

**Table 1.** Characteristics of the four replicates demarcated by beaver enclosure and control treatment. In each replicate, there were four 100-m transects, two on either side of the river (total of 16 transects for the study).

| Treatment/ Replicate | Area (ha) | Linking habitat | No. transects east | No. transects west | River length (m) | % river length tree-lined |
|---|---|---|---|---|---|---|
| Beaver enclosure | | | | | | |
| A | 20 | D, H, GL, W | 2 | 2 | 958 | 84 |
| B | 20 | D, H, W | 2 | 2 | 895 | 62 |
| Control | | | | | | |
| A | 2 | D, H, W | 2 | 2 | 204 | 97 |
| B | 2 | D, H, GL, W | 2 | 2 | 283 | 98 |
| Total | | | 8 | 8 | 2340 | |

Key: D = ditch, H = hedge, GL = green lane, W = woodland.

(e.g. deer) along Finchingfield Brook, which will find their pathways across the landscape restricted, altering their behaviour (e.g. feeding areas) in the unfenced control meadows (Xu et al. 2021). The topography of the sampled enclosure and control meadows was almost completely even (c. slopes <1% gradient) within 10 m of Finchingfield Brook on the east and west sides. The control meadows to the south and north of the enclosures were post-arable grasslands (cropping ceased after 2018) unaffected by the activities of beavers. Adjacent to both post-arable control meadows were existing rough grassland areas (Brown 2022) which could be considered the donor sites for Orthoptera to colonise the establishing beaver enclosure meadows and bolster populations already existing in the reestablishing riparian grassland of the enclosures. Grassland of the enclosures and control meadows was predominantly tall (>50 cm height) and unmanaged before the commencement of the study.

Throughout the duration of the 2024 summer study period there was no active conservation management of any of the sampled grassland. All fields were surrounded by dense hedgerows, ditches and/or woodland by Finchingfield Brook (Table 1, Fig. 2).

*Transect surveys.*—Four 1-m wide × 100-m long transects were established in each of the two beaver enclosure and two control meadow replicates and ran parallel to Finchingfield Brook within 10 m of the bank top (Table 1, Fig. 2). Transects were located along 100-m stretches of Finchingfield Brook which were representative of the vegetation communities of the enclosures and control meadows. In Enclosure B, the evidence of beaver activity was widespread (6 dams, 2 lodges and 6 felled trees, Fig. 3) leading to the creation of a new river channel where water had been impounded behind a dam and spilled out onto the eastern floodplain (Fig. 1A). The transect in this area was along the edge of this lotic channel. Trees felled included willow *Salix* spp. and aspen *Populus tremula* (Linnaeus, 1753). In Enclosure A, there were 5 felled trees but no dams or lodges (Fig. 1). Woody material was present in the channel and did impede flow but not so that water overflowed onto the floodplain similar to Enclosure B's dams.

The transect sampling closely followed the methodology of Gardiner et al. (2005), Gardiner and Hill (2006) and Gardiner and Casey (2024). Adult individuals of all Orthoptera species along all transects were recorded acoustically and visually to determine assemblage composition and species diversity and richness. Each transect was walked at a slow, strolling pace (2 km/hr) once in June, July, August and September 2024 (4 surveys). Nymphs flushed from a 1-m wide band in front of the observer were recorded along all transects. As it is difficult to distinguish between species in the early instars (though not impossible, see Thommen 2021), nymphs of all species were lumped together for recording purposes. With practice, it was relatively easy to ascertain the species of adults without capture (Gardiner and Hill 2006) although some species such as the long-winged conehead *Conocephalus fuscus* (Fabricius, 1793) and *R. roeselii* are significantly under-recorded using visual transects (Gardiner and Hill 2006). A dual visual and acoustic monitoring method has been used by Weiss et al. (2013) to ensure complete coverage of the orthopteran fauna of sites. In the current study, a stridulation monitoring technique was used to record adult males of species which stridulated along the transects at the same time as visual monitoring by flushing. Stridulation monitoring has been used to record cryptic species in Essex and has been found to be effective compared to visual sighting transects and pitfall traps (Harvey and Gardiner 2006, Gardiner et al. 2010). A Magenta Mk4 bat detector (Magenta Electronics Ltd., Burton-on-Trent, Staffordshire, UK) was used in the current study (set at 28 khz to detect ultrasonic bush-crickets, Meyer and Elsner 1996) by the first author (TG) to allow reliable detection of stridulating males up to 20 m away either

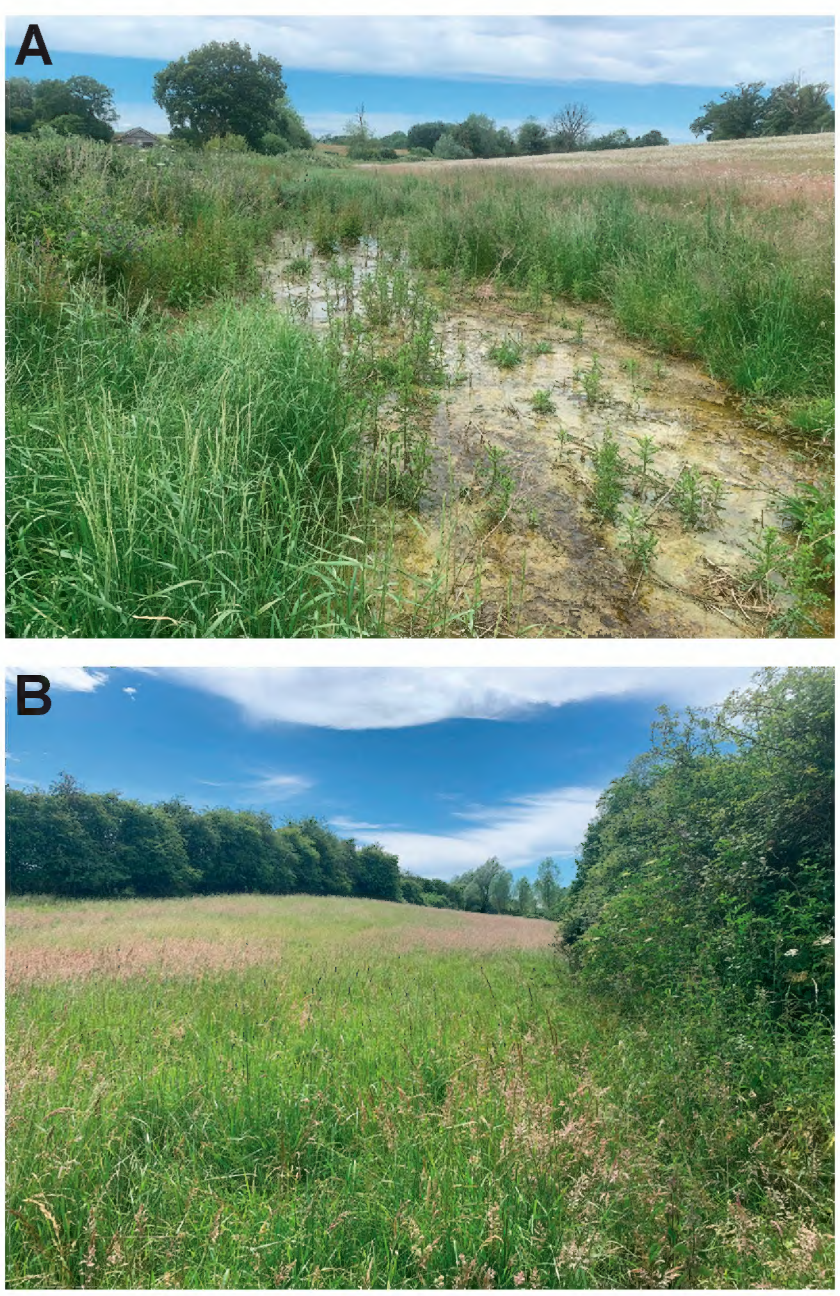


**Fig. 1.** Beaver enclosure B (**A**) with newly created wetland/lotic channel near to a dam and control meadow B (**B**) at Spains Hall © Tim Gardiner.

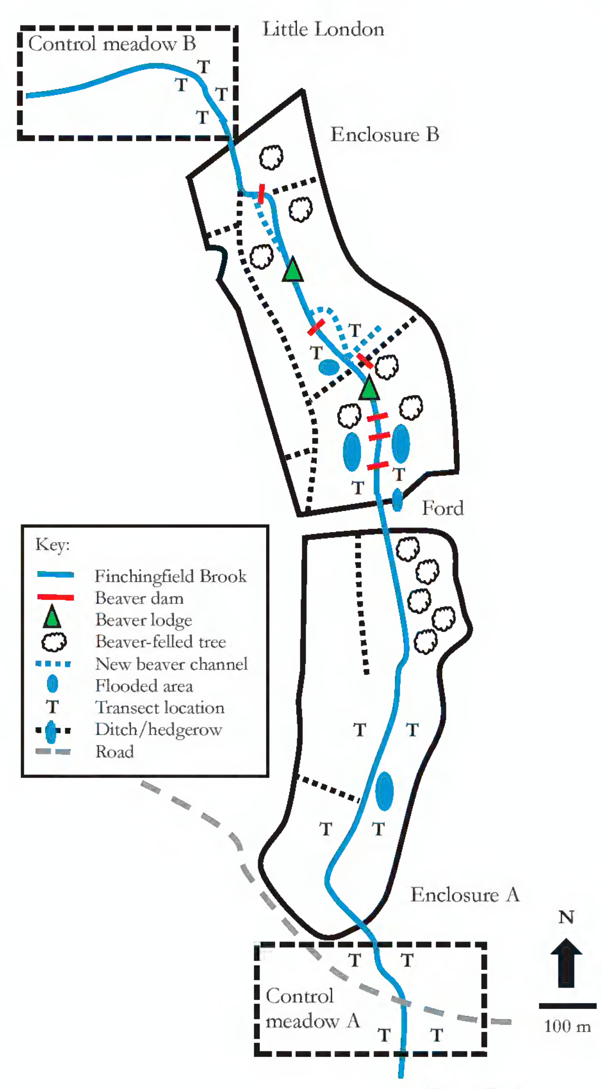


**Fig. 2.** Map of the features of the two fenced beaver enclosures and unfenced control meadows at Spains Hall in Finchingfield, UK.

side of the transect. The weather conditions on survey days were favorable for insect activity, being largely sunny and warm (>17 °C).

*Environmental surveys.*—A total of 40 vegetation heights were recorded at random positions along each of the 16 Orthoptera transects using a 1-m ruler in September 2024. The vegetation species the 1-m ruler touched at ground level at each of the 40 random locations on every transect was recorded to determine the comparative number of hits for different species.

*Statistical analysis.*—All data were square-root transformed to correct for non-normality before analysis (Heath 1995). Significance for all tests was accepted as evidence on the following scale in accordance with Muff et al. 2022: $p$-value >0.1 little or no evidence, 0.05–0.1 weak evidence, <0.05 moderate evidence, <0.01 strong evidence or <0.001 very strong evidence.

*Orthoptera.*—To determine species preferences between beaver enclosure and control meadows all detections of Orthoptera (visual or acoustic) were summed for each replicate for the survey period (4 surveys) to determine the relative abundance of adults of each species in accordance with previous studies (notably, Weiss et al. 2013). Independence of replicate was assumed and data pooled for each one in a similar way to data analysis in other monitoring studies (Nur et al. 1999). Additionally, to test the relationship between different species and vegetation height, all detections of Orthoptera (visual or acoustic) were summed for each 100-m transect section.

Species richness was calculated for each 100-m transect. Assemblage diversity estimates were also calculated using Version 4.1.2. Species Diversity and Richness software (Pisces Conservation Ltd, IRC House, The Square, Pennington, Lymington, Hampshire) from collated data. The Shannon-Wiener Diversity Index (H′, Kent and Coker 1992) was calculated using the total number of individuals recorded for each Orthoptera species in each of the 16 transect sections.

To determine whether the abundance of adults (of all species) and nymphs and vegetation height differed between beaver enclosure and control meadows (treatment) and east and west aspects (aspect), a two-way ANOVA was used for all comparisons. For aspect, data from transects on the east and west side of Finchingfield Brook were compared. To determine the influence of beaver enclosures further, species richness and Shannon-Wiener diversity were compared for beaver enclosures and control transects (treatment) and east and west aspects (aspect) using a two-way ANOVA for all comparisons.

Additionally, to determine whether adults of each species, nymphs and species richness and diversity had significant relationships with vegetation height, linear regression models were run (Heath 1995).

## Results

Nine species of Orthoptera (33% of British native species) were recorded in both the beaver enclosures and control meadows. Two localised (*T. subulata* and common groundhopper *Tetrix undulata* (Sowerby, 1806) and one Essex Red Data List species, common green grasshopper *Omocestus viridulus* (Linnaeus, 1758) were detected in beaver enclosure and control meadows (Fig. 4). The most commonly recorded species were *R. roeselii* (n = 684, 41%) and *Pseudochorthippus parallelus* (Zetterstedt, 1821) (n = 564, 33% of adult detections), followed by *Chorthippus brunneus* (Thunberg, 1815) (n = 130, 8%). Both dark bush-cricket *Pholidoptera griseoaptera* (De Geer, 1773) (n = 86, 5%) and *C. fuscus* (n = 68, 4%). were more infrequent. Scarcer species (<4% of detections) included both groundhoppers (*T. subulata* n = 62, and *T. undulata* n = 57), *O. viridulus* (n = 17) and lesser marsh grasshopper *Chorthippus albomarginatus* (De Geer 1773) (n = 16).

There was moderate evidence ($p < 0.05$) that the abundance of *C. albomarginatus*, *T. subulata* and *T. undulata* was significantly higher in the beaver enclosures compared to the control meadows (Table 2, Fig. 4). Weak evidence existed for higher species diversity ($F = 6.7$, $p = 0.06$) in the beaver enclosures compared to the controls. For *C. fuscus* and *T. subulata*, there was statistical evidence (weak) of higher abundance on the east side of Finchingfield Brook. In the case of *T. subulata*, abundance was significantly higher on the east side of the watercourse in the beaver enclosures than on the west ($F = 11.2$, $p = 0.03$).

In the beaver enclosures, *R. roeselii* was the most abundant orthopteran, comprising c. 38% of the total number of Orthoptera overall (total no. = 843), while *P. parallelus* formed c. 25%. However, in the control meadows *P. parallelus* comprised c. 42% of adult detections and *R. roeselii* c. 43%. In the beaver enclosures, the two groundhoppers, *T. subulata* and *T. undulata* (both species enclosure: c. 7%, control <1%), were in higher abundance in the beaver enclosure assemblages compared to the control grasslands. In Enclosure B (east transects), we noted groundhoppers (both *Tetrix* spp. combined) in June colonising the dry mud of a new river channel established by a beaver dam (Fig. 6), only to disappear after flow returned to the watercourse (in July) during a period of heavy rain (Table 3). Groundhoppers then reappeared later in the summer (August and September) after flows dropped and there was exposed mud once more. On the edge of pooled water in Enclosure B (east side), groundhoppers were consistently observed throughout the surveys (June-September, Table 3).

The combined abundance of the two co-dominant species in the beaver enclosures (*R. roeselii* and *P. parallelus* enclosure:


**Fig. 3.** Beaver enclosure B dam (**A**) and patchy vegetation cover near a lodge (**B**) at Spains Hall © Tim Gardiner.

**Table 2.** Two-way ANOVA F values, significance and statistical evidence shown for differences between means for each Orthoptera species/nymphs and Shannon-Wiener species diversity and richness for treatment (beaver enclosure and control meadow) and aspect (east/west side of river).

| Species | F | Treatment *P* | Evidence | F | Aspect *P* | Evidence |
|---|---|---|---|---|---|---|
| Acrididae (grasshoppers) | | | | | | |
| *Chorthippus albomarginatus* | 9.94 | 0.03 | Moderate | 1.90 | 0.24 | - |
| *Chorthippus brunneus* | 2.81 | 0.17 | - | 3.15 | 0.15 | - |
| *Omocestus viridulus* | 1.13 | 0.35 | - | 0.01 | 0.93 | - |
| *Pseudochorthippus parallelus* | 2.75 | 0.17 | - | 0.07 | 0.80 | - |
| Tettigoniidae (bush-crickets) | | | | | | |
| *Conocephalus fuscus* | 4.06 | 0.11 | - | 5.77 | 0.07 | Weak |
| *Pholidoptera griseoaptera* | 0.26 | 0.64 | - | 1.52 | 0.29 | - |
| *Roeseliana roeselii* | 0.73 | 0.44 | - | 0.18 | 0.69 | - |
| Tetrigidae (groundhoppers) | | | | | | |
| *Tetrix subulata* | 16.33 | 0.02 | Moderate | 7.01 | 0.06 | Weak |
| *Tetrix undulata* | 8.00 | 0.05 | Moderate | 1.57 | 0.28 | - |
| Nymphs (all species) | 0.02 | 0.89 | - | 0.44 | 0.54 | - |
| Species richness | 2.0 | 0.23 | - | 0 | 1.00 | - |
| Species diversity | 6.7 | 0.06 | Weak | 4 | 0.12 | - |
| Vegetation height | 9.50 | 0.04 | Moderate | 2.75 | 0.17 | - |

**Table 3.** Total number of Tetrigidae (both *Tetrix* species combined) in Enclosure B on east transects parallel to a new river channel created by beaver damming and by pools of water on the floodplain.

| Month | River margins | Pool margins | Total |
|---|---|---|---|
| June | 10 | 7 | 17 |
| July | 0 | 11 | 11 |
| August | 19 | 31 | 50 |
| September | 2 | 16 | 18 |
| Total | 31 | 65 | 96 |

63%, control: 85%) may have accounted for their higher species diversity. Vegetation height was significantly lower (F = 9.5, $p$ = 0.04) in the beaver enclosures compared to the control meadows (Tables 2, 4). Vegetation height was typically homogenously tall in the control meadows (only 25 (12.5%) recorded heights < 50 cm) which contrasted with the beaver enclosures where it was lower (87 (43.5%) recorded heights < 50 cm).

At a more localised level, vegetation height influenced the abundance and diversity of Orthoptera. There were moderately significant negative relationships detected for *C. brunneus* (Fig. 5) and *T. subulata* (Table 5), indicating a preference for shorter vegetation in both cases. For species diversity there was also statistical evidence for a significant negative relationship with vegetation height (Table 5, Fig. 5), suggesting more diverse assemblages at lower sward heights (<50 cm).

In both the beaver enclosures in this study, the grasses false oat *Arrhenatherum elatius*, timothy *Phleum pratense* and common bent *Agrostis capillaris* were more frequent in the beaver enclosures, while cock's-foot *Dactylis glomerata* (Linnaeus, 1753), Yorkshire fog *Holcus lanatus* (Linnaeus, 1753) and tall fescue *Lolium arundinacea* (Darbyshire 1993) were more numerous in the control meadows (Table 6). Common comfrey *Symphytum officinale* (Linnaeus, 1753) was found in wetter patches along Finchingfield Brook in the beaver enclosures in some abundance (Table 6). The declining Essex Red Data plant, sneezewort *Achillea ptarmica* (Linnaeus, 1753) was found outside of the standard survey in Enclosure A while water mint *Mentha aquatica* ((Linnaeus), Tucker and Naczi (2006)) and great willowherb *Epilobium hirsutum* (Linnaeus, 1753) were observed in both enclosures.

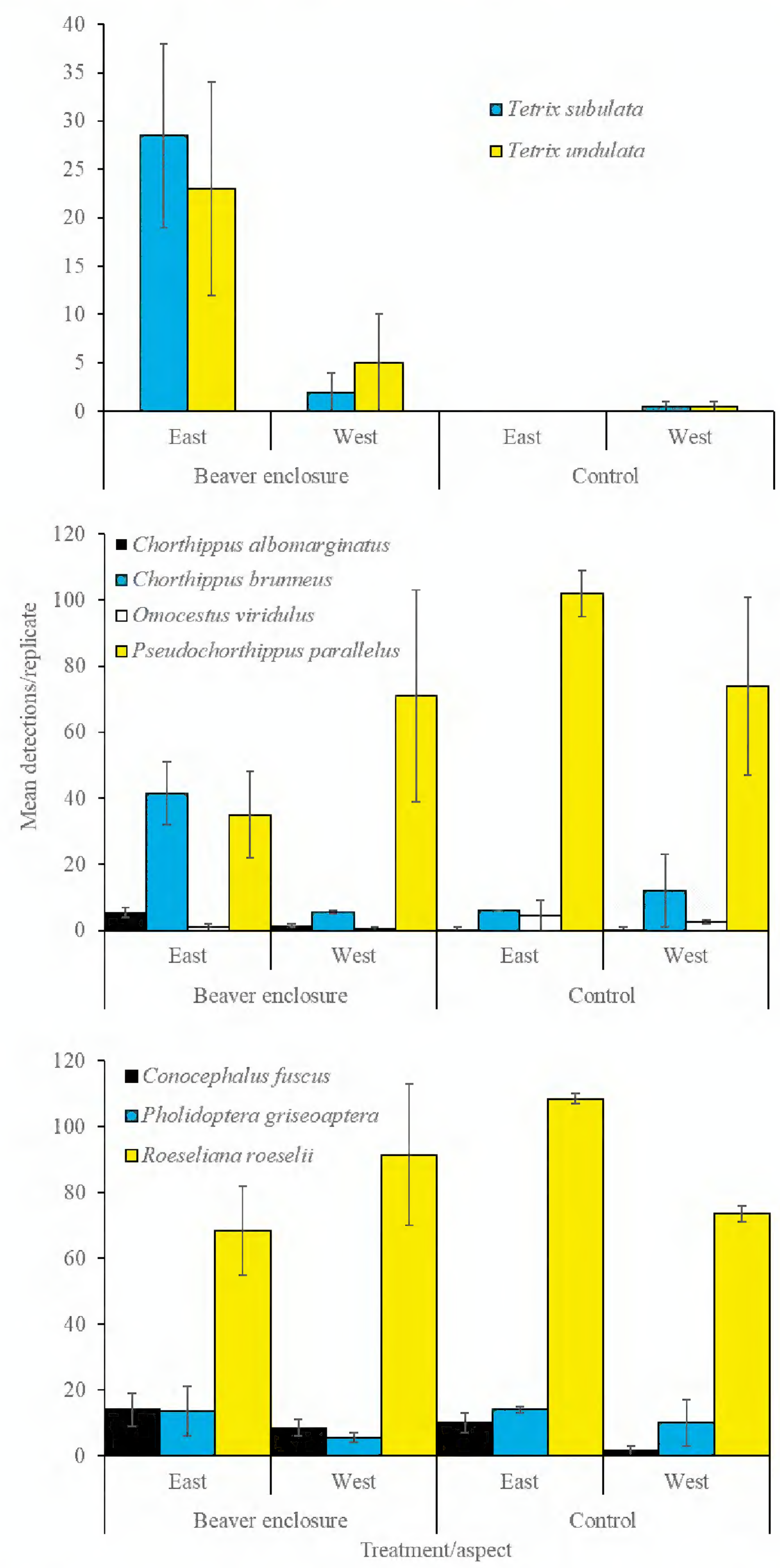


**Fig. 4.** Mean detections (± standard error) in beaver enclosures and controls (east and west aspect shown) for groundhoppers (Tetrigidae - top); grasshoppers (Acrididae - middle) and bush-crickets (Tettigoniidae - bottom).

**Table 4.** Total species count, mean Shannon-Wiener species diversity, richness and mean vegetation height for treatment (beaver enclosure and control meadow) and aspect (east/west side of river), standard error shown.

| Variable | Beaver enclosure | | Control | |
|---|---|---|---|---|
| | East | West | East | West |
| Total species | 9 | 9 | 7 | 9 |
| Species richness | 8.5 ± 0.5 | 7.5 ± 1.5 | 6.0 ± 1.0 | 7.0 ± 1.0 |
| Species diversity | 1.8 ± 0.1 | 1.3 ± 0.3 | 1.2 ± 0.0 | 1.2 ± 0.0 |
| Vegetation height (cm) | 54.5 ± 8.2 | 74.1 ± 2.0 | 81.9 ± 4.7 | 78.0 ± 2.4 |

**Table 5.** Linear regression (all models 1 DF) values for vegetation height (independent variable) paired with Orthoptera nymphs and adults of each species, species diversity/richness and habitat dependent variables. Significance evidence shown for regression model.

| Species | R | F | *p* | Evidence |
|---|---|---|---|---|
| *Chorthippus brunneus* | -0.69 | 12.70 | <0.01 | Strong |
| *Tetrix subulata* | -0.50 | 4.69 | 0.05 | Moderate |
| *Tetrix undulata* | -0.41 | 2.86 | 0.11 | - |
| *Chorthippus albomarginatus* | -0.31 | 1.51 | 0.24 | - |
| *Pseudochorthippus parallelus* | 0.25 | 0.93 | 0.35 | - |
| *Omocestus viridulus* | 0.22 | 0.68 | 0.42 | - |
| *Roeseliana roeselii* | 0.18 | 0.48 | 0.50 | - |
| *Pholidoptera griseoaptera* | -0.11 | 0.18 | 0.68 | - |
| *Conocephalus fuscus* | -0.01 | <0.01 | 0.98 | - |
| Nymphs (all species) | -0.41 | 2.81 | 0.12 | - |
| Species diversity | -0.52 | 5.19 | 0.04 | Moderate |
| Species richness | -0.31 | 1.50 | 0.24 | - |

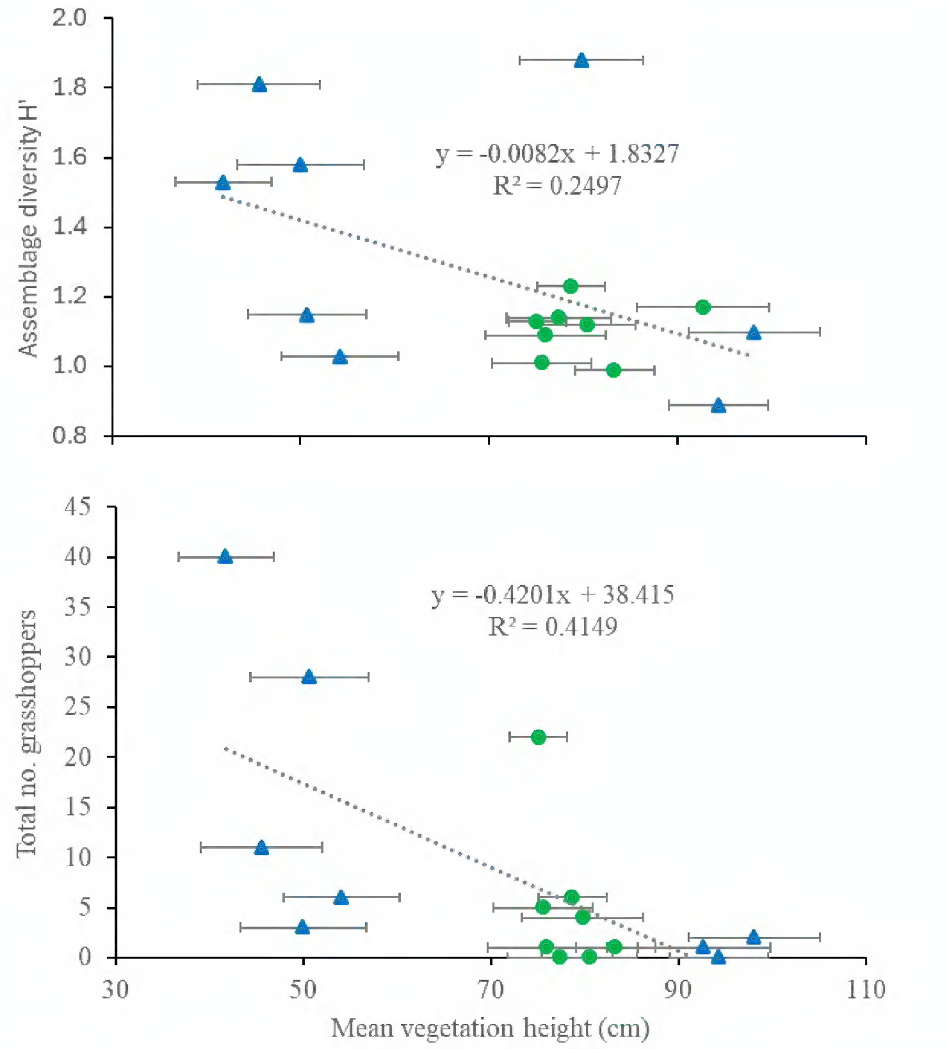


**Fig. 5.** The relationship between vegetation height and the abundance of the field grasshopper *Chorthippus brunneus* (bottom) and assemblage diversity (top), standard error bars shown along with line of best fit and slope statistics. Green circle: control meadow, blue triangle: beaver enclosure.

The mean height of the tussock-forming grasses, *D. glomerata*, *P. pratense* and *L. arundinacea* was >85 cm in both beaver enclosures and control meadows forming homogenously tall grassland where they occurred (Table 6). However, *A. capillaris* and *H. lanatus* had much shorter heights in the beaver enclosures (<50 cm) compared to the control meadows (>60 cm). The height of *S. officinale* was similarly low (<45 cm) in the beaver enclosures where it was much more frequent than the control meadows (Table 6).

## Discussion

Rewilding on arable farmland can lead to fast colonisation by Orthoptera (Gardiner and Casey 2022a, b). Field edge habitats (Cherrill 2015, Arnóczkyné Jakab and Nagy 2022) and ditch banks (Torma et al. 2018) form important corridors in intensively managed farmland maintaining assemblage diversity for Orthoptera and facilitating quick colonization of new beaver meadows in arable landscapes. At Spains Hall, several ditches connected the enclosure transects with surrounding grassland habitats (Fig. 2) which are likely corridors of dispersal to the beaver meadows for ditch bank species such as *C. brunneus*, *C. fuscus*, *P. parallelus* and *R. roeselii* (Torma et al. 2018).

The 9 species recorded at Spains Hall in the controls and beaver enclosures were all recorded at Black Bourn Valley, a Suffolk rewilding site 40 km to the north, which had the same species richness (9 species). Orthopterans inhabiting Black Bourn Valley's post-arable rewilded fields (Gardiner and Casey 2022a, b), were the grasshopper *O. viridulus* and groundhoppers *T. subulata* and *T. undulata*, all species found in the beaver enclosures at Spains Hall in the current study. The similarity of rewilding river valley assemblages to the beaver enclosures suggests that the influence of the mammals may bring positive benefits to damp riparian habitats within just two years. Before grassland reversion, the intensively managed arable fields of the enclosures and control meadows would've been generally denuded of Orthoptera with most species completely absent or in low abundance due to annual ploughing and fertiliser application (Gardiner et al. 2002, Gardiner 2007), leaving narrow (<5 m) unploughed strips either side of Finchingfield Brook and connecting ditches as the only favourable habitat for a baseline population pre-beaver release from which they could colonise the new beaver meadows.

In Germany, a total of 14 species of Orthoptera were recorded in beaver clearings in forests, although *R. roeselii* was absent (Dalbeck 2011), which contrasts with 9 species in the post-arable riparian enclosures in the current study. In both Spains Hall enclosures, *R. roeselii* was the most frequently recorded species perhaps suggesting that open river valley landscapes may be more favorable for this species which was abundant in its preferred tall grassland swards dominated by *A. elatius* and *D. glomerata* (Gardiner 2009).

The initial damming by beavers in Enclosure B (Fig. 3), led to the creation of wetland pools and new river channels running parallel to Finchingfield Brook (Fig. 1). The higher water table led to standing water in this enclosure in particular, although there was wet ground and wetland pools in Enclosure A (Fig. 2). Groundhoppers were observed in some abundance in these areas, largely restricted to wet ground where flooding, occasional tractor wheel ruts and a high-water table led to the dieback of tall grassland swards which were replaced with bare mud. These muddy margins have been noted as a feature of beaver dammed areas in the first two years of activity (Andersen et al. 2024) and are likely important for orthopterans of early successional stages such as groundhoppers which are well known from floodplains (Gardiner and Haines 2008). Groundhoppers may be adapted to the riparian habitats responding to falls in atmospheric pressure by moving to dense vegetation to avoid floods from incoming rainfall (Musiolek and Kočárek 2016), even though they can survive being washed away (Musiolek and Kočárek 2017).

**Table 6.** Frequency of hits (touches) and mean height (± s.e.) for the most abundant plant species (>10 hits) in beaver enclosures and controls.

| Species | No. hits (%) | | Mean height (cm) | |
|---|---|---|---|---|
| | Beaver enclosure | Control | Beaver enclosure | Control |
| *Arrhenatherum elatius* | 39 (20) | 12 (6) | 85.6 ± 6.4 | 105.6 ± 7.7 |
| *Dactylis glomerata* | 23 (12) | 56 (28) | 90.1 ± 7.8 | 92.0 ± 3.0 |
| *Holcus lanatus* | 32 (16) | 79 (40) | 48.2 ± 4.8 | 73.9 ± 2.5 |
| *Symphytum officinale* | 38 (19) | 10 (5) | 34.1 ± 2.4 | 42.9 ± 3.1 |
| *Phleum pratense* | 22 (11) | 12 (6) | 89.6 ± 4.9 | 83.2 ± 7.6 |
| *Lolium arundinaceum* | 11 (6) | 17 (9) | 85.7 ± 9.2 | 95.8 ± 3.9 |
| *Agrostis capillaris* | 10 (5) | 7 (4) | 35.3 ± 5.0 | 61.4 ± 3.2 |

**Fig. 6.** Bare mud in Enclosure B colonised by groundhoppers where a new river channel created by beaver damming had dried out in June 2024 © Tim Gardiner.

These adaptations make them ideally adapted to tolerate the sporadic flooding associated with beaver damming activities. In Enclosure B, we noted groundhoppers in June colonising the dry mud of a new river channel established by a beaver dam (Table 3, Fig. 6), only to completely disappear after flow returned to the watercourse (in July) during a period of heavy rain. Groundhoppers then reappeared later in the summer (August and September) after flows dropped and there was exposed mud once more, a preferred tetrigid habitat around ponds on rewilding sites (Gardiner and Casey 2022a, b).

In Enclosure A where there was beaver felling of trees but no dams or lodges, groundhoppers were much less frequent, being found on wet, muddy ground where a wetland pool had formed in winter and around a few flooded tractor ruts. Small numbers of groundhoppers were also found on wet ground with bare mud around felled trees. In Enclosure A there was woody debris in Finchingfield Brook which appeared to be backing up the flow although it is hard to attribute this to beaver activity with any certainty. The differences in beaver activity between Enclosures A and B indicates that their impacts on riparian environments are patchy in the initial years after reintroduction. This may not be a disadvantage as Orthoptera respond quickly to the patchiness of the floodplain environment, colonising suitable wetland as it develops. If the beavers move on to other areas of the enclosure floodplains, then the wetlands abandoned may develop tall grassland and scrub as succession progresses in the absence of flooding from beaver dams (Andersen et al. 2024).

Tall vegetation (>50 cm) is important in the floodplain mosaic established by beaver damming as habitat for locally scarce damp grassland species such as *O. viridulus* which was found within the first two years of enclosure. Early colonists of beaver enclosure riparian habitats include the bush-crickets, *C. fuscus* and *R. roeselii*, the grasses *A. elatius*, *D. glomerata*, *L. arundinacea* and *P. pratense* providing the tall vegetation cover both species require. The variations in vegetation height facilitated by flooding and destruction of plant cover by high water levels creates patchy grassland which provides shelter for *C. albomarginatus*. Heterogeneity of vegetation height was often seen around beaver dams and and lodges (Fig. 3), where *P. parallelus* and *R. roeselii* could be abundant in taller vegetation while *C. brunneus* inhabited shorter grass.

Assemblage diversity was higher in the shorter swards of the beaver enclosures where early successional Orthoptera species thrive when flooding creates heterogeneity of vegetation cover and suppresses grass growth (Table 4). Livestock grazing (e.g. cattle or sheep) or mosaic grassland mowing can produce a similar diversity in vegetation height (Gardiner 2015). Future management of the enclosures should consider complementing the flooding impacts with grazing or mosaic mowing to produce high quality insect habitats.

Both *C. brunneus* and *T. undulata* were negatively associated with vegetation height being more abundant in short vegetation where vegetation had been suppressed by flooding of the beaver meadows (Table 5, Fig. 5). Habitat preferences of Orthoptera may relate to choice of oviposition site, food preferences and vegetation height (Clarke 1948, Richards and Waloff 1954, Gardiner 2006, 2009).

Short sward patches established by flooding will have excessively hot temperatures (>40°C) similar to hay meadows after cutting (Gardiner and Hassall 2009), unlikely to be favorable for grasshoppers in the absence of 'cool' tussocks in close proximity. Both beaver enclosures had mean vegetation height >50 cm which will have provided Orthoptera with numerous sheltered 'cool' areas of tall vegetation when temperatures may be excessively hot during summer. This behavioural thermoregulation may have accounted for the persistence of species such as *C. brunneus* where basking and egg-laying sites (bare soil) were in close proximity to cooler tall vegetation for shade seeking orthopterans. Along with *C. brunneus*, *P. parallelus* was in relatively high abundance in the beaver enclosures, perhaps preferring the lush *D. glomerata* vegetation for feeding, shelter and oviposition in grass-covered soil (Waloff 1950, Gardiner and Hill 2004), even though the vegetation height was well above the optimal level (10–20 cm) for both grasshoppers (Gardiner et al. 2002). Scrub and trees along the river could be important for species of woody vegetation such as *P. griseoaptera* although they may be affected by removal of their wooded habitat by beaver tree felling in the open valley landscape.

Aspect of the meadows had some influence over *C. fuscus* and *T. subulata* abundance (Table 2), where weak statistical evidence revealed higher abundance in meadows on the east side of the tree-lined river corridor (>60% tree cover, Table 1), particularly for *T. subulata* in the beaver enclosures. It is suggested that shelter from the wind and the exposure to early morning sunlight for Orthoptera on the east side of hedgerows and tree lines are important factors governing their occurrence (Gardiner and Dover 2008) while research on the common spittlebug *Philaenus spumarius* (Linnaeus, 1758) found that temperatures were generally higher on the south-east side of hedgerows compared to the north-west which led to earlier peaks in the abundance of spittle-masses (Ryley and Cherill 2024). Beavers could impact on tree cover in enclosures opening up potentially unfavorable shaded habitat for Orthoptera to colonise when the microclimate becomes warmer which could be significant where the watercourse is tree-lined with a dense overhanging canopy. Further research is needed to investigate the influence of aspect on terrestrial insects along river corridors with beavers.

## Study limitations

*Beaver enclosures.*—The main source of error in this study relates to the presence of only two replicates each for the beaver enclosures and control meadows and the survey only covering one adult Orthoptera season. Future studies should incorporate several enclosures monitored over more than one adult season, although on a field scale this will be expensive due to the length of secure fencing needed and the regular checks of it to ensure there are no escape points. The UK government has also recently authorised the wild release of beavers; therefore, the future focus is likely to move away from captive reintroductions (DEFRA 2025). Enclosure B, which had abundant evidence of beaver activity including 6 dams (dam density 6.7/km), was upstream of Enclosure A where there was no evidence of damming, only tree felling. Therefore, the alteration of water velocity and storage on the floodplain with slower flow due to damming by the upstream Enclosure B beavers may reduce the river favourability for beavers downstream in Enclosure A. Dam density is typically 0.4–1.6 dams/km although it can be as high as 30 dams/km (Graham et al. 2022), usually on rivers <6 m wide and <0.7 m deep (Hartman and Törnlöv 2006). Therefore, Enclosure B has a high density of dams, particularly interesting beaver territories are in areas with substantive woodland cover, although not always (Stringer et al. 2018). Beavers in the open grassland enclosures at Spains Hall may therefore by in uncharacteristic environments with little riparian woodland where activity will be unpredictable.

The observed variability of beaver activity in the two enclosures suggests it is hard to predict how important the influence of damming, lodge building and tree felling will be, consequently desired outcomes for insect assemblages may not be achieved quickly, if at all. A greater independence of enclosures along a river with control plots in between could test interactions between beavers in upper and lower parts of a river catchment providing further evidence of how they react in post-arable environments.

Enclosures also limit beaver impact on the landscape, confining it to a relatively small area (in this case 20 ha in each enclosure) which could prevent successional stages from fully developing due to the widespread flooding of riparian grassland. Beavers can abandon areas in the wider landscape which allows beaver meadows to dry out and develop into tall grassland and scrub, while newly dammed parts of rivers can revert to early successional floodplain habitats with plenty of pools and bare mud in beaver meadows. The absence of deer grazing in the enclosures meant that their pathways and laydown areas with shorter vegetation favourable to grasshoppers (Gardiner and Casey 2022a), were absent. The enclosure fences may also have altered the pathways and grazing areas available to deer in the surrounding control meadows (Xu et al. 2021). Therefore, we should be cautious about applying the study results to wild beaver release locations where herbivore grazing and passage will be unimpeded.

The study also reports the results of the first two years after the beavers were reintroduced which is in the beaver meadow development phase. How the beaver meadows mature in the coming seasons will determine changes to the Orthoptera assemblages. Caution should therefore be exercised in declaring new beaver enclosures successful without longer-term data.

*Survey limitations.*—The visual and acoustic surveying technique used at Spains Hall further developed that used at other sites utilizing acoustic detectors applied for bat surveys (e.g. Gardiner and Casey 2024) to record species in a standardized way (see Newson et al. 2017 and Walcher et al. 2022), which ensured a strong measure of repeatability between observers and surveys (Diwaker et al. 2007). All seven stridulating species were detected using both visual and acoustic survey techniques at Spains Hall. The conehead *C. fuscus* generally has a peak stridulation frequency (30 kHz) beyond the upper range of human hearing (c. 20 kHz, Diwaker et al. 2007) and is virtually undetected by ear without acoustic detection equipment (Gardiner and Casey 2024). It was recorded with a bat detector at Spains Hall in low abundance (17 acoustic detections vs. 51 visual). Estimates of *C. fuscus* abundance are also impacted by visual detection methods where the cryptic nature of the species leads to under-recording and lower species richness estimates (Gardiner and Hill 2006), particularly problematic in taller vegetation (>50 cm) which was prevalent in the control and beaver meadow enclosures.

Other species, such as *R. roeselii* (peak frequency c. 17 kHz), were commonly detected with the bat detector on the surveys (570 acoustic detections vs. 114 visual), suggesting that the method was useful for species with call frequencies close to or within the range of human hearing (the three grasshopper species in this study have a peak frequency limit ≤ 21 kHz; Meyer and Elsner 1996) which may be hard to detect visually in the tall vegetation of the beaver enclosures and control meadows. The use of a bat detector for the acoustic component of the surveying technique ensured standardization, repeatability and detection of orthopterans which may be hard to visually detect in tall grassland (Gardiner et al. 2005).

## Acknowledgements

The authors would like to thank the Spains Hall Estate for supporting the project and giving permission to survey the enclosures and controls, specifically, Sarah Brockless and Archie Ruggles-Brise. The Environment Agency also supported the authors during the project, particularly Christine Freeland. Thanks are extended to the reviewers, Anton Kristin and Thomas Zuna-Kratky, and editors, Axel Hochkirch and Tony Robillard, for constructive feedback on the paper.

## References

Andersen LH, Nummi P, Bahrndorff S (2024) Can beavers help improve terrestrial invertebrate diversity? Frontiers in Ecology and Evolution 12: 1396207. https://doi.org/10.3389/fevo.2024.1396207

Andersen LH, Ransborg C, Pertoldi C, Pagh S, Bahrndorff S (2023) Can reintroduction of beavers improve insect biodiversity? Journal of Environmental Management 337: 117719. https://doi.org/10.1016/j.jenvman.2023.117719

Arnóczkyné Jakab D, Nagy A (2022) How can an intensively used agricultural landscape preserve diversity of Orthoptera assemblages? Journal of Insect Conservation 26: 947–958. https://doi.org/10.1007/s10841-022-00439-7

Brazier RE, Puttock A, Graham HA, Auster RE, Davies KH, Brown CML (2021) Beaver: Nature's ecosystem engineers. WIREs Water 8(1): e1494. https://doi.org/10.1002/wat2.1494

Broad G (2023) Into the wild – exploring the rewilding debate. SBIS Newsletter (Summer 2023), 3–5.

Brown E (2022) Spains Hall Whole Farm Reservoir NbS Book. Atkins Ltd., Oxford, 81 pp. Spains Hall Estate Whole Farm Reservoir Report.pdf.

Bush BM, Wissinger SA (2016) Invertebrates in beaver-created wetlands and ponds. In: D Batzer, Boix D (Eds) Invertebrates in Freshwater Wetlands: An International Perspective on their Ecology. Cham: Springer International Publishing, 411–449. https://doi.org/10.1007/978-3-319-24978-0_12

Campbell-Palmer R, Gow D, Campbell R, Dickinson H, Girling S, Gurnell J, Halley D, Jones S, Lisle S, Parker H, Schwab G, Rosell F (2016) The Eurasian Beaver Handbook: Ecology and Management of *Castor fiber*. Pelagic Publishing, London, 214 pp. https://doi.org/10.2307/jj.28833745

Campbell-Palmer R, Schwab G, Girling S, Lisle S, Gow D (2015) Managing wild Eurasian beavers: a review of European management practices with consideration for Scottish application. Scottish Natural Heritage Commissioned Report No. 812. Scottish Natural Heritage, Inverness.

Carver S, Convery I (2021) Rewilding: time to get down off the fence? British Wildlife 32(4): 246–255.

Cherrill A (2015) Large-scale spatial patterns in species richness of orthoptera in the Greater London area, United Kingdom: relationships with land cover. Landscape Research 40(4): 476–485. https://doi.org/10.1080/01426397.2014.902922

Clarke EJ (1948) Studies in the ecology of British grasshoppers. Transactions of the Royal Entomological Society of London 99: 173–222. https://doi.org/10.1111/j.1365-2311.1948.tb01235.x

Cunningham JM, Calhoun AJK, Glanz WE (2007) Pond-breeding amphibian species richness and habitat selection in a beaver-modified landscape. The Journal of Wildlife Management 71: 2517–2526. https://doi.org/10.2193/2006-510

Dalbeck L (2011) Biberlichtungen als Lebensraum für Heuschreckegn in Wäldern der Eifel. Articulata 26(2): 97–108.

Darbyshire SJ (1993) Realignment of *Festuca* subgenus *Schedonorus* with the Genus *Lolium* (Poaceae). Novon 3(3): 239. https://doi.org/10.2307/3391460

DEFRA (2025) Policy paper. Wild release and management of beavers in England. DEFRA, London. Wild release and management of beavers in England - GOV.UK.

De Geer C (1773) Mémoires pour servir à l'histoire des insectes, vol. 3. Pierre Hesselberg, Stockholm. 696 pp., 44 pls. http://books.google.com/books?id=emJNAAAAYAAJ [Accessed on 06.02.2022]

Dempsey B (2021) Everything under control? Comparing Knepp Estate rewilding project with 'traditional' nature conservation. PLOS ONE 16(6): e0241160. https://doi.org/10.1371/journal.pone.0241160 [PMID: 34061859; PMCID: PMC8168866].

Diwakar S, Jain M, Balakrishnan R (2007) Psychoacoustic sampling as a reliable, non-invasive method to monitor orthopteran species diversity in tropical forests. Biodiversity and Conservation 16: 4081–4093. https://doi.org/10.1007/s10531-007-9208-0

Fabricius JC (1793) Supplementum Entomologiae Systematicae 2. Apud. Proft et Storch, Hafniae.

Fargeaud K, Gardiner T (2018) The response of Orthoptera to grazing on flood defense embankments in Europe. Journal of Orthoptera Research 27: 53–61. https://doi.org/10.3897/jor.27.25183

Fartmann T, Freienstein FM, Helbing F, Scherer G, Poniatowski D (2024) A box quadrat for standardised sampling of Orthoptera in open habitats: design, handling, applications and baseline data. Global Ecology and Conservation 55: e03217. https://doi.org/10.1016/j.gecco.2024.e03217

Forbes H, Ball K, McLay F (2015) Natural flood management handbook. Scottish Environment Protection Agency, Stirling, Scotland.

Gardiner T (2006) The impact of grassland management on Orthoptera populations in the UK. Unpublished PhD thesis, University of Essex.

Gardiner T (2007) Orthoptera of crossfield and headland footpaths in arable farmland. Journal of Orthoptera Research 16: 127–133. https://doi.org/10.1665/1082-6467(2007)16[127:OOCAHF]2.0.CO;2

Gardiner T (2009) Hopping back to happiness? Conserving grasshoppers on farmland. VDM Verlag, Saarbrücken.

Gardiner T (2015) Sea Wall Biodiversity Handbook. RPS, Cambridge.

Gardiner T, Casey D (2022a) Orthoptera in the early stages of post-arable rewilding in south-east England. Journal of Orthoptera Research 31(2): 163–172. https://doi.org/10.3897/jor.31.82317

Gardiner T, Casey D (2022b) The implications for Orthoptera of grazing in arable wilding schemes. British Wildlife 34(1): 8–17.

Gardiner T, Casey D (2024) Topographic heterogeneity influences diversity and abundance of Orthoptera in a rewilding scheme. Journal of Orthoptera Research 33(2): 255–266. https://doi.org/10.3897/jor.33.119897

Gardiner T, Dover J (2008) Is microclimate important for Orthoptera in open landscapes? Journal of Insect Conservation 12: 705–709. https://doi.org/10.1007/s10841-007-9104-7

Gardiner T, Haines K (2008) Intensive grazing by horses detrimentally affects orthopteran assemblages in floodplain grassland along the Mardyke River Valley, Essex, England. Conservation Evidence 5: 38–44.

Gardiner T, Hassall M (2009) Does microclimate affect grasshopper populations after cutting of hay in improved grassland? Journal of Insect Conservation 13: 97–102. https://doi.org/10.1007/s10841-007-9129-y

Gardiner T, Hill J (2004) Feeding preferences of *Chorthippus parallelus* (Orthoptera: Acrididae). Journal of Orthoptera Research 13: 197–203. https://doi.org/10.1665/1082-6467(2004)013[0197:FPOCPO]2.0.CO;2

Gardiner T, Hill J (2006) A comparison of three sampling techniques used to estimate the population density and assemblage diversity of Orthoptera. Journal of Orthoptera Research 15: 45–51. https://doi.org/10.1665/1082-6467(2006)15[45:ACOTST]2.0.CO;2

Gardiner T, Hill J, Chesmore D (2005) Review of the methods frequently used to estimate the abundance of Orthoptera in grassland ecosystems. Journal of Insect Conservation 9: 151–173. https://doi.org/10.1007/s10841-005-2854-1

Gardiner T, Pye M, Field R, Hill J (2002) The influence of sward height and vegetation composition in determining the habitat preferences of three *Chorthippus* species (Orthoptera: Acrididae) in Chelmsford, Essex, UK. Journal of Orthoptera Research 11: 207–213. https://doi.org/10.1665/1082-6467(2002)011[0207:TIOSHA]2.0.CO;2

Gardiner T, Seago B, Benton T, Dobson J (2010) The use of bat detectors reveals a widespread population of Grey Bush-cricket *Platycleis albopunctata* at Colne Point and St Osyth naturists' beach. Essex Naturalist 27: 209–213.

Garrido P, Naumov V, Söderquist L, Jansson A, Thulin C-G (2022) Effects of experimental rewilding on butterflies, bumblebees and grasshoppers. Journal of Insect Conservation 26: 763–771. https://doi.org/10.1007/s10841-022-00420-4

Gordon IJ, Manning AD, Navarro LM, Rouet-Leduc J (2021a) Domestic livestock and rewilding: Are they mutually exclusive? Frontiers in Sustainable Food Systems 5: 550410. https://doi.org/10.3389/fsufs.2021.550410

Gordon IJ, Pérez-Barbería FJ, Manning AD (2021b) Rewilding lite: Using traditional domestic livestock to achieve rewilding outcomes. Sustainability 13: 3347. https://doi.org/10.3390/su13063347

Graham HA, Puttock A, Chant J, Elliott M, Campbell-Palmer R, Anderson K, Brazier RE (2022) Monitoring, modelling and managing beaver (*Castor fiber*) populations in the River Otter catchment, Great Britain. Ecological Solutions and Evidence 3: e12168. https://doi.org/10.1002/2688-8319.12168

Greenaway TE (2006) Knepp Castle Estate baseline ecological survey. English Nature Research Reports, No. 693. Peterborough, English Nature.

Hagenbach JJ (1822) Symbola faunae insectorum Helvetiae exhibentia vel species novas vel nondum depictas. J. Georgii Neukirch, Basileae. http://publikationen.ub.uni-frankfurt.de/volltexte/2006/103489/ [Accessed on 06.02.2022]

Halley DJ, Saveljev AP, Rosell F (2021) Population and distribution of beavers *Castor fiber* and *Castor canadensis* in Eurasia. Mammal Review 51: 1–24. https://doi.org/10.1111/mam.12216

Hartman G, Törnlöv S (2006) Influence of watercourse depth and width on dam-building behaviour by Eurasian beaver (*Castor fiber*). Journal of Zoology 268: 127–131. https://doi.org/10.1111/j.1469-7998.2005.00025.x

Harvey P, Gardiner T (2006) Pitfall trapping of scarce Orthoptera at a coastal nature reserve in Essex, UK. Journal of Insect Conservation 10: 371–373. https://doi.org/10.1007/s10841-006-9013-1

Heath D (1995) An Introduction to Experimental Design And Statistics For Biology. CRC. https://doi.org/10.1201/b12546

Hering D, Gerhard M, Kiel E, Ehlert T, Pottgiesser T (2001) Review study on near-natural conditions of Central European mountain streams, with particular reference to debris and beaver dams: results of the "REG Meeting" 2000. Limnologica 31: 81–92. https://doi.org/10.1016/S0075-9511(01)80001-3

Hooker J, Foxley T, Stone EL, Lintott PR (2024) Re-establishing historic ecosystem links through targeted species reintroduction: Beaver-mediated wetlands support increased bat activity. Science of the Total Environment 2951: 175661. https://doi.org/10.1016/j.scitotenv.2024.175661 [Epub2024Aug21 PMID: 39173747]

Horak J, Vavrova E, Chobot K (2010) Habitat preferences influencing populations, distribution and conservation of the endangered saproxylic beetle *Cucujus cinnaberinus* (Coleoptera: Cucujidae) at the landscape level. European Journal of Entomology 107: 81–88. https://doi.org/10.14411/eje.2010.011

Kent M, Coker P (1992) Vegetation Description and Analysis: a Practical Approach. Chichester, John Wiley and Sons.

Larsen A, Larsen JR, Lane SN (2021) Dam builders and their works: Beaver influences on the structure and function of river corridor hydrology, geomorphology, biogeochemistry and ecosystems. Earth-Science Reviews 218: 103623. https://doi.org/10.1016/j.earscirev.2021.103623

Law A, Bunnefeld N, Willby NJ (2014) Beavers and lilies: Selective herbivory and adaptive foraging behaviour. Freshwater Biology 59(2): 224–232. https://doi.org/10.1111/fwb.12259

Linnaeus CN (1753) Species Plantarum 2: 1034. 856 pp.

Linnaeus CN (1758) Systema Naturae per Regna tria naturae (10th ed.). Laurentii Salvii, Holmiae, 824 pp. http://www.biodiversitylibrary.org/item/10277#page/3/mode/1up [Accessed on 06.02.2022]

Mourant A, Lecomte N, Moreau G (2018) Indirect effects of an ecosystem engineer: how the Canadian beaver can drive the reproduction of saproxylic beetles. Journal of Zoology 304: 90–97. https://doi.org/10.1111/jzo.12506

Muff S, Nilsen EB, O'Hara RB, Nater CR (2022) Rewriting results sections in the language of evidence. Trends in Ecology & Evolution 37: 203–210. https://doi.org/10.1016/j.tree.2021.10.009

Musiolek D, Kočárek P (2016) Weather-dependent microhabitat use by *Tetrix tenuicornis* (Orthoptera: Tetrigidae). The Science of Nature 103: 68. https://doi.org/10.1007/s00114-016-1393-9

Musiolek D, Kočárek P (2017) Effect of substrate on the risk of being washed away by floods for the Groundhoppers *Tetrix subulata* and *Tetrix tenuicornis* (Orthoptera: Tetrigidae). River Research and Applications 33: 1071–1078. https://doi.org/10.1002/rra.3167

Newson SE, Bas Y, Murray A, Gillings S (2017) Potential for coupling the monitoring of bush-crickets with established large-scale acoustic monitoring of bats. Methods in Ecology and Evolution 8: 1051–1062. https://doi.org/10.1111/2041-210X.12720

Nummi P (1989) Simulated effects of the beaver on vegetation, invertebrates and ducks. Annales Zoologici Fennici 26: 43–52.

Nur N, Jones SL, Geupel GR (1999) A statistical guide to data analysis of avian monitoring programs. U.S. Washington, D.C, Department of the Interior, Fish and Wildlife Service, BTP-R6001-1999, 54 pp.

Orazi V, Hagge J, Gossner MM, Müller J, Heurich M (2022) A biodiversity boost from the Eurasian Beaver (*Castor fiber*) in Germany's oldest National Park. Frontiers in Ecology and Evolution 10: 873307. https://doi.org/10.3389/fevo.2022.873307

Raye L (2015) The early extinction date of the beaver (*Castor fiber*) in Britain. Historical Biology 27(8): 1029–1041. https://doi.org/10.1080/08912963.2014.927871

Richards OW, Waloff N (1954) Studies on the biology and population dynamics of British grasshoppers. Anti-Locust Bulletin 17: 1–182.

Romansic JM, Nelson NL, Moffett KB, Piovia-Scott J (2020) Beaver dams are associated with enhanced amphibian diversity via lengthened hydroperiods and increased representation of slow-developing species. Freshwater Biology 66(3): 481–494. https://doi.org/10.1111/fwb.13654

Rosell F, Bozsér O, Collen P, Parker H (2005) Ecological impact of beavers *Castor fiber* and *Castor canadensis* and their ability to modify ecosystems. Mammal Review 35: 248–276. https://doi.org/10.1111/j.1365-2907.2005.00067.x

Ryley GHT, Cherrill A (2024) The effect of thermal microclimates on the nymphal development and abundance of the Common Meadow Spittlebug, *Philaenus Spumarius* (Hemiptera: Cicadomorpha: Aphrophoridae), in hedgerows. The British Journal of Entomology and Natural History 37(3): 170–182.

Sowerby J (1806) The British miscellany; or, Coloured figures of new, rare, or little known animal subjects: many not before ascertained to be inhabitants of the British Isles: and chiefly in the possession of the author, James Sowerby. R. Taylor & Co., London, 136 pp. https://doi.org/10.5962/bhl.title.41623

Stringer AP, Blake D, Genney DR, Gaywood MJ (2018) A geospatial analysis of ecosystem engineer activity and its use during species reintroduction. European Journal of Wildlife Research 64: 1–9. https://doi.org/10.1007/s10344-018-1195-9

Stringer AP, Gaywood MJ (2016) The impacts of beavers *Castor* spp. on biodiversity and the ecological basis for their reintroduction to Scotland, UK. Mammal Review 46: 270–283. https://doi.org/10.1111/mam.12068

Thommen D (2021) Jugendstadien der Heuschrecken der Schweiz. Bern, Haupt Verlag AG, 416 pp.

Torma A, Bozsó M, Gallé R (2018) Secondary habitats are important in biodiversity conservation: a case study on orthopterans along ditch banks. Animal Biodiversity and Conservation 41(1): 97–108. https://doi.org/10.32800/abc.2018.41.0097

Thunberg CP (1815) Hemipterorum maxillosorum genera illustrata plurimisque novis speciebus ditata ac descripta. Mémoires de l'Académie Impériale des Sciences de St. Pétersbourg 5: 211–301.

Tree I (2017) The Knepp Wildland project. Biodiversity 18(4): 206–209. https://doi.org/10.1080/14888386.2017.1407258

Tucker AO, Naczi RFC (2006) *Mentha*: An overview of Its classification and relationships. In: BM Lawrence (Ed.) Mint: The Genus *Mentha*. CRC Press, Florida, 1–39.

van Klink R, WallisDeVries MF (2018) Risks and opportunities of trophic rewilding for arthropod communities. Philosophical Transactions of the Royal Society B, Biological Sciences 373: 20170441. https://doi.org/10.1098/rstb.2017.0441

Walcher R, Hussain RI, Sachslehner L, Zaller JG, Arnberger A, Frank T (2022) Assessing grasshopper communities in mountainous meadows – a comparison of a visual-acoustic and a novel, purely acoustic soundscape method. Entomologia Experimentalis et Applicata 170: 895–901. https://doi.org/10.1111/eea.13209

Wallace C (2018) The Impacts of a Rewilding Project on Pollinator Abundance and Diversity at a Local Scale. Unpublished Masters Thesis, University of Sussex.

Waloff N (1950) The egg pods of British short-horned grasshoppers (Acrididae). Proceedings of the Royal Entomological Society of London 25: 115–126. https://doi.org/10.1111/j.1365-3032.1950.tb00088.x

Weiss N, Zucchi H, Hochkirch A (2013) The effects of grassland management and aspect on Orthoptera diversity and abundance: site conditions are as important as management. Biodiversity and Conservation 22: 2167–2178. https://doi.org/10.1007/s10531-012-0398-8

Willby NJ, Law A, Levanoni O, Foster G, Ecke F (2018) Rewilding wetlands: Beaver as agents of within-habitat heterogeneity and the responses of contrasting biota. Philosophical Transactions of the Royal Society, B: Biological Sciences 373(1761): 20170444. https://doi.org/10.1098/rstb.2017.0444

Wilson JB, Bremner-Harrison S (2025) A systematic literature review investigating the association between biodiversity and beaver lodges. Mammal Review 55: e12363. https://doi.org/10.1111/mam.12363

Wright JP, Jones CG, Flecker AS (2002) An ecosystem engineer, the beaver, increases species richness at the landscape scale. Oecologia 132: 96–101. https://doi.org/10.1007/s00442-002-0929-1

Wróbel M (2020) Population of Eurasian beaver (*Castor fiber*) in Europe. Global Ecology and Conservation 23: e01046. https://doi.org/10.1016/j.gecco.2020.e01046

Xu W, Dejid N, Herrmann V, Sawyer H, Middleton AD (2021) Barrier Behaviour Analysis (BaBA) reveals extensive effects of fencing on wide-ranging ungulates. Journal of Applied Ecology 58: 690–698. https://doi.org/10.1111/1365-2664.13806

Zahner V, Hanöffer S, Schurli C, Müller S (2006) Beaver induced structure change along a stream in bavaria and its influence on fish fauna and indicator beetles, in Proceedings of the Abstracts from the 4th European Beaver Symposium, (Freising: Fachhochschule Weihenstephan).

Zetterstedt JW (1821) Orthoptera Sueciae. Litteris Berlingianis, Lundae. http://books.google.com/books?id=kwYPAQAAIAAJ [Accessed on 06.02.2022]